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Climate-induced changes in forest disturbance and vegetation

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RECENT concern over the ecological effects of future trace-gas-induced climate change has accelerated efforts to understand and quantify climate-induced vegetation change[1-9]. Here we discuss new and published climate-model results indicating that global warming favours increased rates of forest disturbance, as a result of weather more likely to cause forest fires (drought, wind and natural ignition sources), convective wind storms, coastal flooding and hurricanes. New sensitivity tests carried out with a vegetation model indicate that climate-induced increases in disturbance could, in turn, significantly alter the total biomass and compositional response of forests to future warming. An increase in disturbance frequency is also likely to increase the rate at which natural vegetation responds to future climate change. Our results reinforce the hypothesis[6] that forests could be significantly altered by the first part of the next century. Our modelling also confirms the potential utility of selected time series of fossil pollen data for investigating the poorly understood natural patterns of century-scale climate variability.

We wish to highlight the need to incorporate realistic disturbance regimes in model assessments of future vegetation change. Higher rates of disturbance can increase the rate at which forests are opened up for new trees that are better adapted to modified climate conditions. Disturbance thus acts to short-circuit the slower process of forest-gap initiation and overturn through old-age mortality[10,11]. Increased rates of forest disturbance also increase the relative proportion of early successional (rapid-growing, shade-intolerant) and disturbance-adapted trees on the landscape. The form and rate of climate-induced change in vegetation can thus depend on the frequency of disturbance[10,11].

In northern mid-latitude forests, the chief forms of non-anthropogenic catastrophic disturbance are fire and catastrophic windthrow[12,13]. The incidence of these events is proportional to the incidence of 'disturbance weather', primarily summer/autumn drought and thunderstorms (lightning and wind) for fire[14] and large-scale thunderstorms for windthrow[12]. To a lesser degree, disturbance weather also includes tornadoes, hurricanes and floods. Climate-model results indicate that warmer climates tend to be characterized by more frequent disturbance weather for several reasons. Latitudinal temperature contrasts and atmospheric eddy energy tend to be weakened as climate warms, thus decreasing temperature variability on all timescales[15]. This may lead to longer runs of consecutive hot days without cool breaks during future growing seasons. In addition, the increased moisture-holding capacity of warmer atmospheres should be associated with greater precipitation variability[15]. As climates become warmer, temperature-driven increases in potential evapotranspiration will probably exceed increases in precipitation at the warmer low and mid-latitudes[16,17]. All of these factors combine to make the probability of summer/autumn drought, and thus fire, more likely during warmer periods[15-18].

Model results also indicate that higher temperatures and greater atmosphere moisture loading produce significant increases in penetrating convection (Fig. 1). This increase implies a significant change in the intensity and frequency of large thunderstorms. Several studies using general circulation model (GCM) results also indicate that tropical storms and hurricanes are likely to be strengthened under warm climate conditions[19,20]. Climate theory and model results therefore support recent analyses of palaeoecological fire-frequency records[21-23], which offer a clear indication that the magnitude and frequency of disturbance weather could be significantly higher during periods of hemispheric warmth than during cooler times.

We used the mixed-species (72 total), mixed-age stochastic stand-simulation model FORENA to simulate the effects of climate change on four forest types in eastern North America (Table 1). FORENA is a widely used and tested model that simulates the processes controlling the establishment, growth and death of trees on a 1/12-ha plot[5,24]. We modified the program so that we could specify the probability of catastrophic disturbance or death of all trees on a given plot. We also specified that

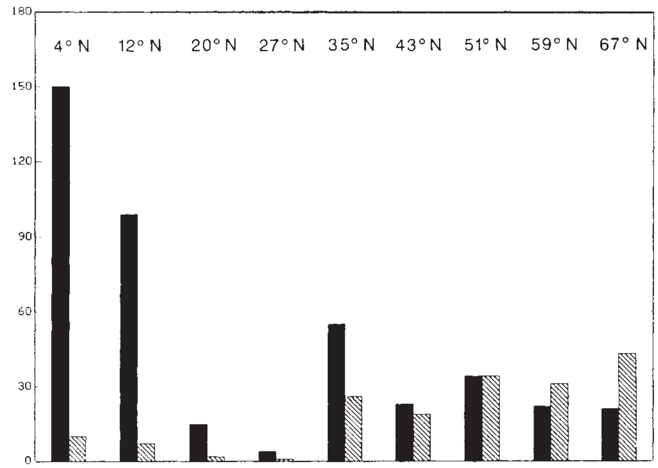

FIG. 1 Increase in annual average penetrative mass flux that is due to moist convection through the 300-mbar level as a function of latitude in an equilibrium $2\times CO_2$ climate-change simulation[25]. Values represent mass flux × height (solid bars in 10^{12} kg m s^{-1}), and percentage increase in mass flux (striped bars). An increase in mass flux to higher levels in the atmosphere is likely in a world warmed by trace gases. This increase will probably translate into more intense thunderstorms, wind, lightning activity (C. Price and D. Rind, manuscript in preparation) and forest disturbance at mid- to high latitudes.

TABLE 1 Sites at which forest growth was simulated

State or province	Latitude	Longitude	Dominant modern-day forest constituents
N Wisconsin	45.0° N	90.0° W	*Pinus, Acer, Quercus*
S Quebec	47.9° N	75.0° W	*Abies, Picea, Betula*
NE Michigan	44.8° N	83.6° W	*Pinus, Quercus, Picea*
S Illinois	39.0° N	89.0° W	*Quercus, Carya*

a plot had to remain undisturbed for a period of 20 regeneration years before another disturbance could occur. We carried out two types of sensitivity experiments. In the first set (the 'step-function' experiments), we compared pairs of perturbation (with a disturbance increase) and nonperturbation (without a change in disturbance) runs. In both of these runs, simulated forest was grown from bare ground under present-day climate[4] for 800 years to characterize the natural variability of the simulated forest. At year 800, a single climate variable was then changed in a single step to a new mean climate and the simulation run for a further 400 years. In each perturbation experiment, we changed the probability of catastrophic disturbance from 0.00 to 0.01 (equivalent to a realistic frequency of about 1 plot-destroying fire every 115 years, when the 20-year regeneration period is factored in) at year 800; a 0.00 probability was maintained throughout each nonperturbation run.

We examined three types of climate change separately in our step-function experiments: (1) a 1 °C temperature increase; (2) a 2 °C increase; (3) a 15% decrease in precipitation. Changes of these magnitudes could easily have occurred within the late Quaternary and could occur in the future. In our second set of experiments (the 'transient' experiments), we also grew forest from bare ground under observed climate for 800 years. From year 800 to year 900, we linearly changed the mean monthly climate (temperature and precipitation) to simulated equilibrium $2 \times CO_2$ (twofold increase in CO_2) levels[4,25] and then held the climate constant until year 1600. Our rate of change was slightly less than the scenario 'A' transient response modelled by Hansen *et al.*[25]. As before, the nonperturbation runs contained no change in disturbance probability, whereas the perturbation experiments contained step-function increases (from 0.00 to 0.01) in the probability of disturbance at year 800. We used the same relatively drought-insensitive soil in all our runs[5], and averaged the results from 40 random plots into a single time series for each model run.

Selected summary results from sites in the mixed conifer-hardwood forest of Wisconsin and the southern boreal forest of Quebec (Fig. 2) illustrate our results, which are supported by our other experiments, not shown here. An increase in forest disturbance will probably produce climate-induced vegetation change that is greater than, or equal to, the same climate-induced change in the absence of an altered disturbance regime. In many cases, this enhanced change is due to the rapid increases in the

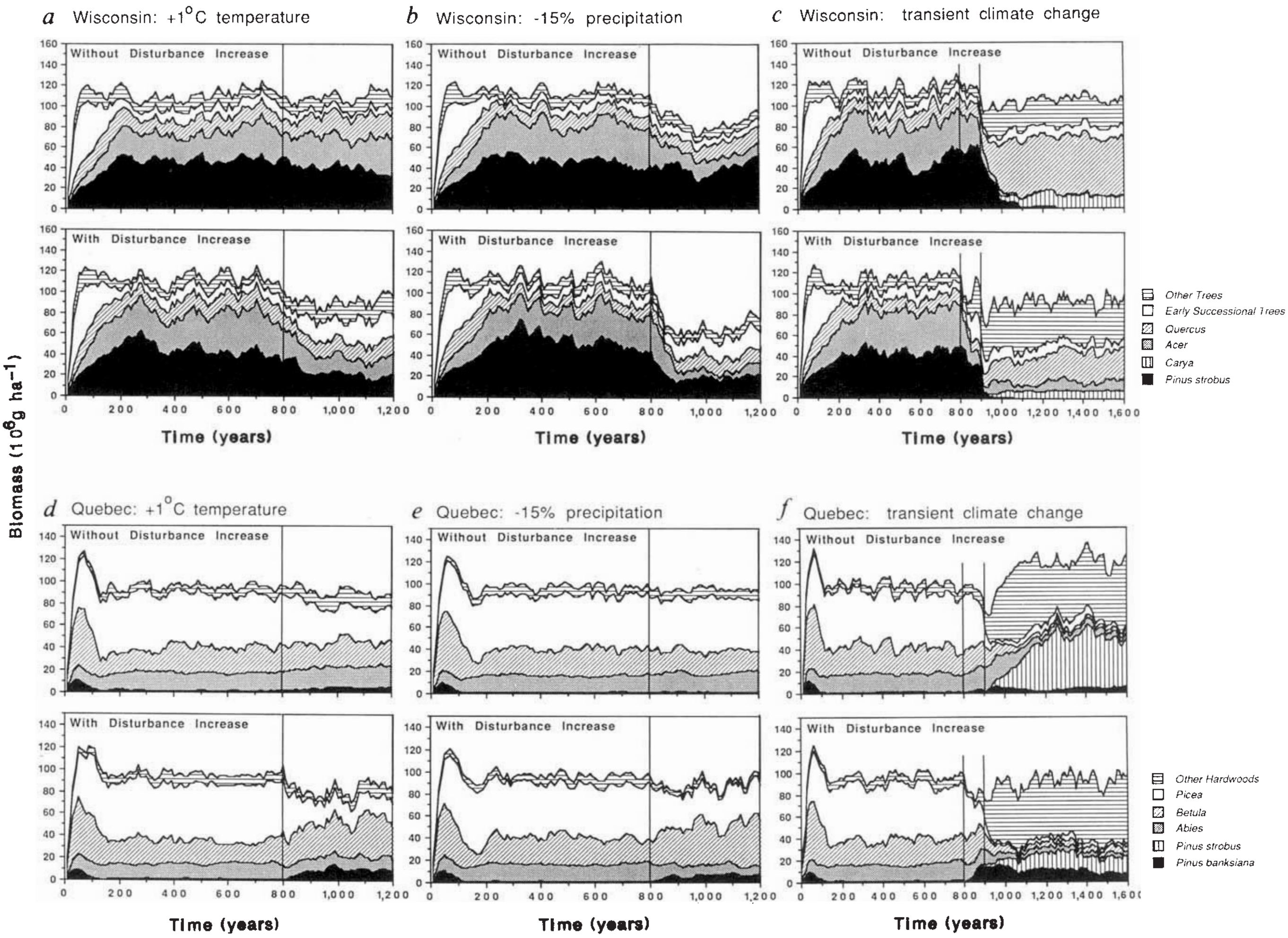

FIG. 2 Simulated changes in species composition in forests at two of the sites we investigated in eastern North America: *a–c* in Wisconsin, *d–f* in southern Quebec (see Table 1). Each plot consists of a nonperturbation simulation (without a change in disturbance) and a perturbation (with a change in disturbance) simulation.

abundances of early successional species that occur in response to increased disturbance frequency. In some cases (such as Figs 2*a*, *d* and *e*), a step-function change in climate alone did not cause a significant change in simulated biomass, whereas the same climate change coupled with an increase in forest disturbance resulted in a significant effect on the forest.

Not only did altered disturbance regimes tend to cause significant changes in simulated forest composition, but they also tended to accelerate the rate of forest response to climate change. The increase in forest disturbance never led to a slower response. In the case of the transient experiments, vegetation change generally lagged behind the initiation of climate change by 50–100 years, in the absence of an increased frequency of disturbance. In these same transient nonperturbation runs, the simulated vegetation took at least 200–250 years to achieve equilibrium conditions under the $2\times CO_2$ climate. By contrast, the presence of an increased rate of forest disturbance resulted in vegetation change that more closely tracked the initiation and timing of climate change. In all of the transient-perturbation experiments, the simulated vegetation took <180 years to regain equilibrium after the initiation of climate change at year 800.

Our results should not be construed as predictions for the future trace-gas-warmed world, but instead highlight the need for improved vegetation models (both on a regional and a global scale) that include realistic disturbance routines that are interactively linked to climate variability. Other factors (such as soil dynamics, seed sources, direct trace-gas effects, pollution, pests, pathogens, forest management and the accumulation of fire fuels) must be considered[8,23]. Rapid climate change could speed tree mortality and forest dieback[5], thus increasing the rate of fuel buildup and the probability of disturbance by fire.

Our results have immediate applicability for the future, but they also indicate that vegetation change may have closely tracked past climate change in the presence of disturbance regimes that were suitably rapid and sensitive to climate variability. This supports the careful use of fossil-pollen data in the examination of past century to millenium-scale climate change[26–28]. Such studies should be important for assessing the rapid climate and vegetation changes that may occur in the future. Our results thus contrast somewhat with earlier forest-modelling results[10], which indicated that pollen records may not be capable of resolving climate change within 100–150 years. This assertion is undoubtedly true for many sites with insensitive forest-disturbance regimes, but should not hinder the continued use of fossil pollen data in the study of the patterns and causes of century-scale climate and vegetation variability. □

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Evaluation of an acidification model with data from manipulated catchments in Norway

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INTERNATIONAL efforts to control the emissions of the acidifying compounds SO_2 and NO_x to the atmosphere, and to establish critical loads, are in part aimed at predicting the long-term response of soils and waters to changes in acid deposition. Estimation of future long-term trends in acidification requires the use of models, the strict verification of which requires years or decades to determine whether predictions match observed responses. Experimental manipulations with whole ecosystems provide data with which predictive models can be evaluated. The MAGIC model[1,2] is a widely used, intermediate-complexity, process-oriented model for soil and water acidification in catchments. Here we follow up a preliminary application[3] of the model to the first two years of data from the manipulated catchments of the RAIN (Reversible Acidification In Norway) project[4]. We use a more extensive four-year data set as inputs to a new version of the model. The four-year record provides a much more rigorous test of the predictive ability of the model because these data show major changes in runoff chemistry due to the experimental change in deposition. Sensitivity analysis shows that MAGIC is successful at predicting future acidification.

The RAIN project comprises two parallel large-scale manipulations in which acid deposition is experimentally changed at whole catchments[4]. At Sogndal in western Norway, a 7,200-m^2 pristine headwater catchment (SOG2) is artificially acidified by the addition of 70–100 meq m^{-2} yr^{-1} H_2SO_4. At Risdalsheia in southern Norway, ambient acid precipitation is excluded by means of a 1,200-m^2 roof, and clean precipitation is applied beneath the roof. Two untreated catchments at each site provide reference data.

The processes incorporated in the MAGIC model include atmospheric deposition, sulphate adsorption, cation exchange, CO_2 dissolution, precipitation and dissolution of aluminium, chemical weathering, uptake and release of cations by vegetation and export in runoff. The model produces long-term reconstructions and predictions of soil and streamwater chemistry in response to given acid deposition scenarios[1,2]. It uses an aggregated approach in two ways: (1) a myriad of chemical and biological processes active in catchments are modelled by a few readily described processes; (2) an averaged set of parameters is used to describe the soil properties within the catchment.

Whereas standard precipitation gauges provide adequate estimates of integrated inputs to catchments and the outputs in runoff are integrated at the weir, estimates of the soil parameters